

CHROMOSOME COUNTS AND TAXONOMY OF  
*MENTZELIA THOMPSONII* (LOASACEAE)

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ABSTRACT

The species *Mentzelia thompsonii* Glad was published in 1976 based solely on herbarium material, and it is the only species in *Mentzelia* section *Trachyphytum* that has not been examined cytogenetically. Here we report that *M. thompsonii* is diploid ( $2n = 18$ ), making it the easternmost diploid species in section *Trachyphytum* and the only one that does not occur in California. The diploid status and edaphic specialization of *M. thompsonii* suggest that it is a paleoendemic isolated from other diploids in *Trachyphytum* by specialization during Pleistocene climate change. Our investigations have also uncovered confusion in the literature and herbaria regarding the taxonomy of *M. thompsonii* and its overall place within *Mentzelia*. *Mentzelia thompsonii* has been synonymized with *Mentzelia humilis* (Urb. & Gilg) J. Darl. (a member of section *Bartonia*) in several prominent databases and herbaria. To the contrary, our studies reveal that *M. thompsonii* is distinct from *M. humilis*; furthermore, as a unique component of Colorado Plateau diversity, it is critical for inferences of biogeographic evolution in section *Trachyphytum*.

Key Words: *Acrolasia humilis*, biogeography, diploid, Mancos Shale, *Mentzelia humilis*, *Mentzelia thompsonii*, Pleistocene climate change, polyploidy.

*Mentzelia thompsonii* Glad (Fig. 1) is a small annual confined to the Colorado Plateau of the southwestern United States. Its range extends from the Four Corners region north along the Utah-Colorado border to the Uinta Basin (Fig. 2). The species is an edaphic endemic, usually occurring on barren, salty soils derived from the Mancos Shale Formation (Glad 1976; Holmgren et al. 2005; Brokaw 2009). *Mentzelia thompsonii* is one of the most recently described species in section *Trachyphytum* (Glad 1976), and its evolutionary significance within this group is only now becoming apparent (Brokaw and Hufford 2010a, b). Prior to cytogenetic surveys of the group, only eight North American species were recognized in section *Trachyphytum* (Loasaceae) (Darlington 1934). However, the discovery of extensive polyploidy (Zavortink 1966) and coincident reproductive barriers subsequently led to the recognition of over 20 species in the southwestern United States alone. *Mentzelia thompsonii* was described ten years after Zavortink's (1966) biosystematic revision of *Trachyphytum*, and it is the only North American species

currently lacking a chromosome count. Recent work has suggested that section *Trachyphytum* represents a monophyletic group exhibiting complicated polyploid evolution (Hufford et al. 2003; Brokaw and Hufford 2010a, b), and verification of the ploidal level of *M. thompsonii* is vital to the interpretation of molecular evolution and gene flow in the group.

The goals of the study were: 1) to collect chromosome data for *M. thompsonii* and 2) to develop a set of chromosomally vouchered molecular and morphological samples for systematic analyses. While these cytogenetic analyses have been essential to determine *M. thompsonii*'s role in the polyploid complexes of section *Trachyphytum*, our investigations have also led to new insights regarding the biogeography of *Trachyphytum* and resolved confusion in the literature and herbaria regarding the taxonomy and validity of *M. thompsonii*.

MATERIALS AND METHODS

Populations examined in this study were selected to represent the northwestern (Uinta Co., UT, Brokaw 234) and southeastern (San Juan Co., NM, Brokaw 345) limits of the

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FIG. 1. Habit of *Mentzelia thompsonii* Glad. Photograph courtesy of W. A. Weber (University of Colorado).

distribution of *M. thompsonii*. Chromosome counts were made from field-collected microsporocytes fixed in Farmer's solution (3 parts 95% ethanol: 1 part glacial acetic acid) at the time of voucher collection. Following the procedures outlined by Windham (2000), fixed materials were stored at  $-20^{\circ}\text{C}$  and transferred to 70% ethanol immediately before making slides. Dissected anthers were macerated in a drop of 1% acetocarmine stain, which was mixed 1:1 with Hoyer's solution prior to setting the cover slip and squashing. Slides were examined with an Olympus BH-2 phase contrast microscope, and representative cells were photographed using Kodak Technical Pan 2415 film. The voucher specimens, Brokaw 234 (WS375612) and Brokaw 345 (WS375773), have been deposited at the Marion Ownbey Herbarium (WS). Additional duplicate vouchers have been sent to ACU and COLO.

## RESULTS AND DISCUSSION

Analyses of microsporocytes undergoing meiosis revealed that the chromosome number of both the northwestern and southeastern popula-

tions of *M. thompsonii* is  $n = 9$ . The chromosomes consistently formed nine bivalents during the reductional division (Fig. 3a) and these segregated normally during anaphase II to produce four daughter cells containing nine chromatids each (Fig. 3b). The base chromosome number of *Mentzelia* section *Trachyphytum* is  $x = 9$ , making *M. thompsonii* a diploid. It is the easternmost diploid in the section and the only one that does not occur in California (Fig. 2). Further, it is the only diploid species whose current distribution does not overlap with any other diploid in *Trachyphytum*.

## Evolutionary Ecology

The discovery that *Mentzelia thompsonii* is diploid has important implications for our understanding of biogeography and evolution in section *Trachyphytum*. The lineage of *M. thompsonii* is nested within the section *Trachyphytum* clade (Brokaw and Hufford 2010a) leading to the most parsimonious hypothesis that *M. thompsonii* represents a range extension far from the California origin of the *Trachyphytum* diploids. The section has its greatest species richness and representatives of all its major clades in southern California. The polyploid taxa generally have larger distributions, extending further north and east than those of diploids (Zavortink 1966). Prior to our investigation of *M. thompsonii*, only polyploid taxa were known to have gotten as far east as the Colorado Plateau. Given that polyploids are derived from diploids and thus more recently evolved, analyses of *Trachyphytum* lacking *M. thompsonii* would suggest that range expansions were associated novel trait combinations acquired during or following polyploidization. However, the geography of the diploid *M. thompsonii* represents a major exception to this generalization, suggesting that other factors must be considered.

Patterns of edaphic specialization in *Trachyphytum* may partly explain the disjunct range of *M. thompsonii*. Only two other species in *Trachyphytum*, the tetraploid *M. mollis* M. Peck and the octoploid *M. packardiae* Glad, occur entirely outside California; both are limited to unusual soils (Glad 1975, 1976). Although soils were not available to her for chemical analyses, Glad (1976) first noted that shales and grey clays of the Mancos Formation were commonly listed as substrates on specimen labels for *M. thompsonii*. With a wider sampling of populations, it is now evident that *M. thompsonii* is limited almost exclusively to the Mancos Shale and other Cretaceous marine sediments of the Colorado Plateau (Holmgren et al. 2005; Brokaw 2009). Thus, all three *Trachyphytum* species absent from California appear to be associated with substrate specialization.

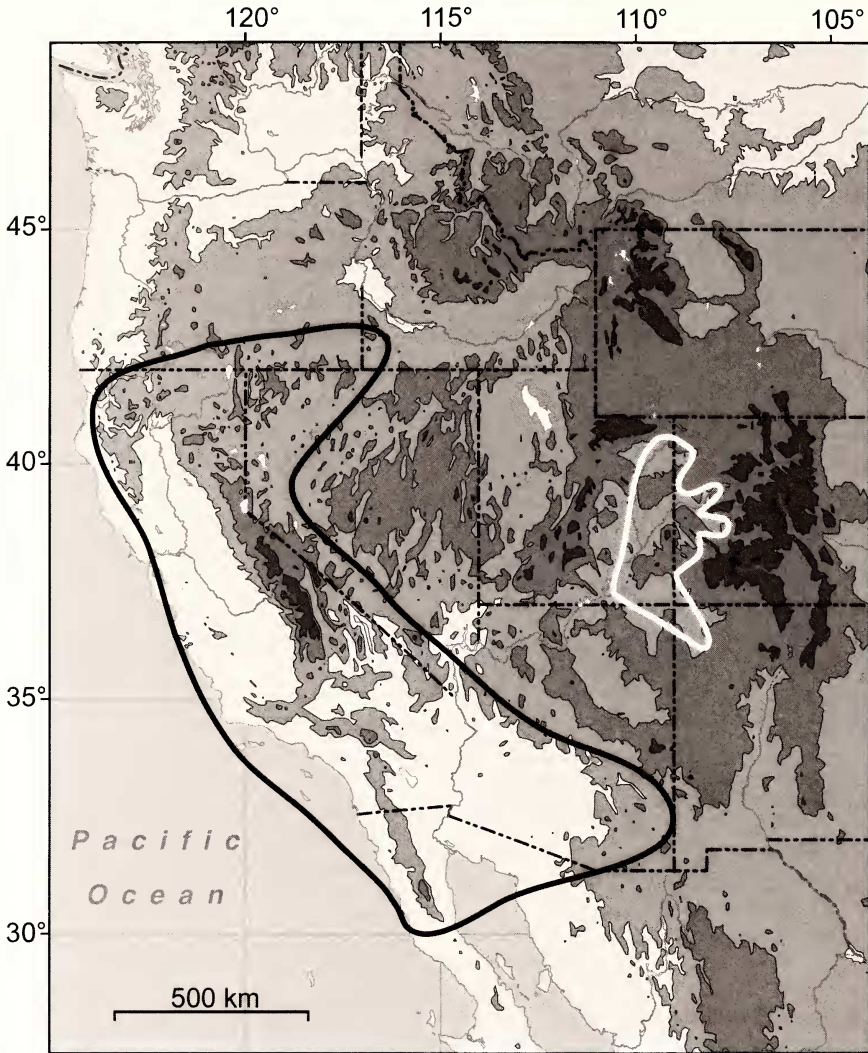


FIG. 2. Range of *Mentzelia thompsonii* in eastern Utah, western Colorado, and Four Corners region (white) and combined ranges of all other diploid species in *Mentzelia* section *Trachyphytum* in California, southern Oregon, southwestern Idaho, western Nevada, southwestern Arizona, and northwestern Mexico (black).

These observations suggest that the simplest biogeographic hypothesis (a one-way expansion from California) may be insufficient to fully explain species distributions in *Trachyphytum*. The range of *M. thompsonii* shows that diploids have accomplished substantial range expansion outside of California. The current abundance of polyploids in intervening regions of the Great Basin and western Colorado Plateau suggest that a similar distribution of ancestral diploids is at least plausible. It is possible that diploid populations formerly in this region have been displaced by competition. This line of reasoning, coupled with observed edaphic specialization, suggests that *M. thompsonii* may be a paleoendemic, i.e., a species isolated through extinctions of close relatives (Stebbins and Major 1965). Major migrations and extinctions of diploid

populations could have been driven by dramatic shifts in vegetation during Pleistocene climate change (Dynesius and Jansson 2000; Thompson and Anderson 2000; Minnich 2007). During vegetational shifts, the ancestors of *M. thompsonii* may have persisted in northeastern portions of the diploid ranges by specializing for edaphically stressful habitats where most competing vegetation was excluded.

It is likely that shifting diploid ranges during the Pleistocene facilitated hybridization, leading to the extensive generation of allopolyploids in *Trachyphytum* documented by Brokaw and Hufford (2010b). *Mentzelia thompsonii* is one of the few diploids in *Trachyphytum* lacking allopolyploid descendents (Brokaw and Hufford 2010b), which is not surprising considering its current isolation from other extant diploids. The

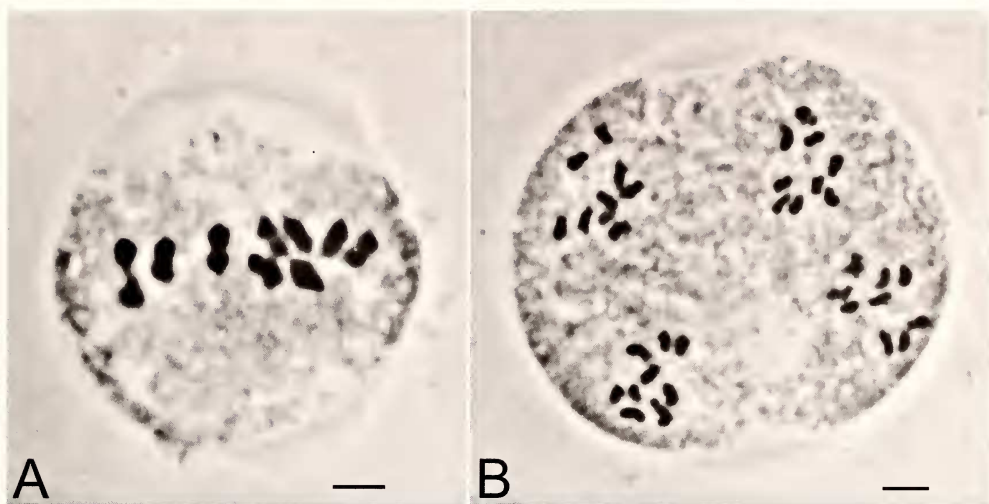


FIG. 3. Chromosomes of *Mentzelia thompsonii* (Brokaw 234) at: A) Metaphase I cell showing nine pairs of chromosomes; B) Anaphase II cell showing four daughter nuclei each containing nine chromatids. Scale bars = 5  $\mu$ m.

species almost certainly had fewer opportunities than most diploids for allopolyploid hybridizations in Pleistocene ice age refugia. However, molecular data have implicated *M. thompsonii* in one introgressional event without polyploidization (Brokaw and Hufford 2010a, b). Brokaw and Hufford (2010a) showed evidence of recombination between nuclear genes of *M. thompsonii* and the Sonoran Desert diploid *M. affinis* Greene, suggesting gene flow between these species. Although *M. thompsonii* and *M. affinis* are not currently sympatric, populations of *M. affinis* approach the range of *M. thompsonii* more closely than those of any other diploid in *Trachyphytum*. *Mentzelia affinis* occurs in southern and western Arizona, separated from the nearest *M. thompsonii* populations (in the Four Corners region) by less than 400 km. The suitability of the intervening habitat during the Pleistocene is unclear, but it is interesting to note that a similar geographic pattern has been observed in the genus *Boechera* (Brassicaceae). In this instance, microsatellite data (Windham et al. unpublished) reveal that *B. perennans* (S. Watson) W. A. Weber (with a southern Arizona range similar to *M. affinis*) has hybridized with *B. pallidifolia* (Rollins) W. A. Weber, a Colorado Plateau endemic that reaches its southern limit near the Four Corners (like *M. thompsonii*). The striking similarity of these two cases suggests that genetic interactions between species occupying the warm deserts of southern Arizona and the cool deserts of the Four Corners region may be more common than previously supposed.

Molecular data have revealed that unexpected interactions between species (like those inferred between *M. thompsonii* and *M. affinis*) are relatively common in *Mentzelia* section *Trachy-*

*phytum* (Brokaw and Hufford 2010a, b). These provide intriguing evidence that Pleistocene migrations have contributed to complicated patterns of molecular evolution, ecological specialization, and a burst of allopolyploid speciation (Brokaw and Hufford 2010a, b). The discovery that *M. thompsonii* is diploid adds another piece to the puzzle, allowing us to view our biogeographic hypotheses in a new light and critically examine the effects of geographic isolation on species evolution in *Mentzelia* section *Trachyphytum*.

#### Taxonomic Status

*Mentzelia thompsonii* is a poorly known taxon, rarely collected and confined to unusual substrates in a region of the United States that is only now receiving the botanical exploration it deserves (Heil et al. in press). This largely explains why it was overlooked by both previous monographic treatments of *Trachyphytum* (Darlington 1934; Zavortink 1966). Not only has this led to the delayed cytogenetic study of *M. thompsonii*, but it has also contributed to a complicated nomenclatural history and, ultimately, to the synonymization of the taxon in prominent databases and herbaria. In fact, *M. thompsonii* is still listed as "not accepted" by the Integrated Taxonomic Information System (ITIS 2011) and the PLANTS Database (USDA-NRCS 2011).

Through a series of nomenclatural and taxonomic errors, *M. thompsonii* (Fig. 4) has been incorrectly synonymized with *M. humilis* (Urb. & Gilg) J. Darl. (Fig. 5), a distantly related member of section *Bartonia*. The initial confusion in the taxonomy of *M. thompsonii* stems from a long-



FIG. 4. Holotype of *Mentzelia thompsonii* Glad.

running disagreement between authors who recognize *Trachyphytum* as a section of the genus *Mentzelia* (Torrey and Gray 1840; Urban and Gilg 1900; MacBride 1918; Darlington 1934; Thompson and Roberts 1974; Hufford et al. 2003) and authors who segregate the group as the genus *Acrolasia* (Presl 1831; Rydberg 1903; Davidson 1916; Weber and Wittman 2001). Following Rydberg's (1903) recircumscription of *Acrolasia*, the entity now known as *M. thompsonii* was first described and published as *Acrolasia humilis* by Osterhout in 1922. The epithet *humilis* had been used previously in *Mentzelia* for a taxon treated by Urban & Gilg (1900) as a variety of *M. pumila* Torr. & A. Gray. Subsequently, Darling-

ton (1934) raised *M. pumila* var. *humilis* Urb. & Gilg of section *Bartonia* to the rank of species as *M. humilis*. Unfortunately, she also treated *A. humilis* and *M. humilis* as homotypic and incorrectly synonymized the name *Acrolasia humilis* under *Mentzelia humilis*.

When Glad (1976) named *M. thompsonii*, she did not mention *Acrolasia humilis*, a name that, nevertheless, could not have been transferred to *Mentzelia* because of Darlington's (1934) earlier elevation of *M. pumila* var. *humilis* to species status. Thus, *M. thompsonii* became the accepted name (in treatments recognizing *Trachyphytum* as a section of *Mentzelia*; e.g., Holmgren et al. 2005) for the species originally described as *Acrolasia*



FIG. 5. Lectotype of *Mentzelia humilis* (Urb. & Gilg) J. Darl. Specimen on right side of sheet is the lectotype (C. Wright 214, 1849) mounted with the non-type specimen (H. N. Patterson s.n., 1875) on the left.

*humilis*. Subsequently, the nomenclatural combination *A. thompsonii* (Glad) W. A. Weber, was proposed to accommodate use of *Acrolasia* in treatments of the Rocky Mountain flora (Weber 1984). However, rediscovery of the original description and holotype of *A. humilis* led to synonymization of *A. thompsonii* and a return to the use of *A. humilis* in later treatments (Weber and Wittman 1992). The final taxonomic error occurred when Kartesz (1999) repeated Darlington's (1934) incorrect synonymy of *A. humilis* with *M. humilis* and went on to designate *M. thompsonii* and *A. thompsonii* as synonyms of *M. humilis*.

Our reconstruction of the taxonomic history of *M. thompsonii* indicates that a failure to consult type specimens has played a major role in the current taxonomic confusion surrounding this species. Even cursory examination of types of *M. thompsonii* and *M. humilis* (Figs. 4 and 5, respectively) reveals that these names do not represent the same taxon. Given the new evidence from cytology and molecular phylogenetics (Brokaw and Hufford 2010a) we hope that earlier taxonomic misinterpretations will be put to rest. *Mentzelia thompsonii* is a distinct species with a unique phylogenetic history and ecological niche,

and it is an important piece of the evolutionary puzzle that is *Mentzelia*.

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